Symphyodon leiocarpus, sp. nov. (Symphyodontaceae, Musci) from Thailand, Classified in the New Subgenus Macrothamniopsis

HIROYUKI AKIYAMA^{1*} AND HIROMI TSUBOTA²

¹Museum of Nature and Human Activities, Hyogo, Yayoigaoka-6, Sanda-shi, Hyogo 449-1546, Japan. *akiyama@hitohaku.jp (author for correspondence); ²Miyajima Natural Botanical Garden, Graduate School of Science, Hiroshima University, 1156-2 Mitsumaruko-yama, Miyajima-cho, Hatsukaichi-shi, Hiroshima 739-0543, Japan

Symphyodon leiocarpus, sp. nov., previously reported under the name Symphyodon oblongifolius, is described from Thailand and Myanmar. The longer axillary hairs, upright capsules with smooth exothecial cells, superficial stomata, and larger spore size suggest its remote relationship to other members of the genus. Based on a molecular phylogenetic analysis using sequences of chloroplast rbcL gene, a new subgenus, Symphyodon subg. Macrothamniopsis, is established to accommodate the species. Morphological comparisons with related genera, especially those of the Hylocomiaceae and Symphyodontaceae, are also discussed briefly.

Key words: *rbcL*, *Symphyodon leiocarpus*, *Symphyodon* subg. *Macrothamniopsis*, Symphyodontaceae, Thailand

Doi (Mt.) Inthanon, the highest peak in Thailand, has long been known to support one of the richest bryophyte floras in Asia (Dixon 1932, 1935, Horikawa & Ando 1964, Kitagawa 1967a, b, Noguchi 1972a, 1973, Ogawa *et al.* 1961, Touw 1968). The upper elevations are covered by well-preserved evergreen montane forests. In addition, mossy forests are developed around the summit and in places over 1800 m (Hara 2003).

Among the bryophytes known from Doi Inthanon are a number of species endemic to the mountain and species with severely restricted distributions, such as *Curvicladium kurzii* (Kindb.) Enroth, *Dixonia orientalis* (Mitt.) H. Akiyama & Tsubota, *Noguchiodendron sphaerocarpum* (Nog.) Ninh & Pócs, *Penzigiella cordata* (Harv.) M. Fleisch., *Pinnatella amblyphylla* Enroth, and *Pseudotrismegistia undulata* (Broth. & Yasuda) H. Akiyama & Tsubota. Among these, *Symphyodon*, a representative of the Himalayan

bryophyte element, contains a high diversity of species, which characterizes the flora of Doi Inthanon. Nine species of *Symphyodon* have been reported from Chiang Mai and six of them are from the upper elevations of Doi Inthanon (He & Snider 2000).

One of us (Akiyama), with permission from the Royal Forest Department of Thailand, was able to study the bryophyte flora at the upper elevations of Doi Inthanon in December 2000. Later in 2008 (March and December), Akiyama again visited Doi Inthanon as a member of a cooperative research project between Kyoto University and Maejo University. Parts of the results based on the collections have been published in separate papers (Akiyama 2007, Akiyama & Tsubota 2001, 2004).

Among the collections, we noticed a curious moss with the gametophytic features of *Symphyodon*, but lacking the characteristic echinate or

spinose capsules. Superficial stomata on the neck of the capsules and larger spores also separated it from other species of Symphyodon (Fig. 1). The plants, which we describe below as Symphyodon leiocarpus, were abundant on the base of tree trunks and on the branches of shrubs in the undergrowth along the Summit and Angka trails around the summit area as well as along the Kew Mae Pan Nature Trail. From our field observations, the new species is not rare in the local mossy forests. Symphyodon leiocarpus was also found growing on branches of tall, emergent trees in the upper montane forest at 1600–1700 m altitude. After checking previous reports on the moss flora of the mountain, it became clear that Symphyodon leiocarpus had previously been reported under the name of Symphyodon oblongifolius (Renauld & Cardot) Broth. [Basionym: Leptohymenium oblongifolium Renauld & Cardot. Type: India orientalis, Sikkim, Darjeeling, L. Stevens s.n.] (Touw 1968, He & Snider 1992, 2000).

Touw (1968) reported *S. oblongifolius* from four localities in Chiang Mai County including Doi Inthanon (see paratypes below). Later, Si He (2009, internet resource) cited three specimens of Touw's collection as *S. oblongifolius*, but did not refer to others collected from Doi Inthanon. He & Snider (1992, 2000) excluded the species in their revision of the genus, mainly because they were not able to locate the type specimen of *S. oblongifolius* in their search through specimens in BM, NY and other herbaria. He & Snider (1992, 2000) therefore left the taxonomic treatment for future investigation. Since that time the species has not been fully reexamined.

The main purpose of this paper is to settle the identity of *Symphyodon leiocarpus* through morphological comparisons and by molecular phylogenetic analysis with related genera.

Morphological Investigations

Comparison with Symphyodon oblongifolius

We attempted to find the type specimen of *Symphyodon oblongifolius* by requesting the help of curators and keepers of the herbaria BM, H, L, NY and PC, in which Renauld's collections might

have been deposited, but like He & Snider (1992, 2000) we were unable to locate it. Although the identity of S. oblongifolius cannot be know with certainty in the absence of a type specimen, we attempted to characterize it from the original description (Renauld & Cardot 1896) and from an additional description by Gangulee (1977) who claimed to have checked the type specimen. Accordingly, Symphyodon oblongifolius can be characterized as follows: 1) shoots irregularly pinnately branched, 2) leaves elliptic-oblong, concave, rounded but gradually pointed to the apex, 3) laminal cells linear, more or less prorate at upper corners, and 4) costa very short. These features fit well with those of typical species of Symphyodon, and it seems reasonable that Brotherus (1907) transferred the species from Leptohymenium to Symphyodon. Although the gametophytes are not diverse among the species of Symphyodon and gametophytic features are often scarcely useful to distinguish individual species, the Symphyodon leiocarpus has the following features (Fig. 1) not observed in S. oblongifolius: 1) shoots more or less regularly bi- or tripinnately branched, 2) leaves ovate-lanceolate, concave, obtuse or broadly acute, 3) laminal cells linear, evenly thick walled, and totally smooth, and 4) costa often reaching half of leaf length, more or less forked. We therefore conclude that Symphyodon oblongifolius and the plants we name S. leiocarpus represent two different species.

Comparison with other species of Symphyodon

According to detailed generic descriptions on Symphyodon by He & Snider (2000) and our own observations, Symphyodon leiocarpus and other members of the genus share a number of features as follows: Plants dioicous; central strands of stems absent or weakly developed; alar regions of stem and branch leaves slightly differentiated with a small numbers of quadrate cells; costae short and double; perichaetia terminal on short branches and becoming extensively elongate after fertilization to form distinctive vaginulae (Fig. 1 c & d); upper portions of setae distinctly mammillose; capsules erect and ovoid with long beaked opercula; peristomes of the Neckera-type

and exostome teeth lack dorsal median furrows; endostome reduced, with low basal membranes and linear segments (sometimes absent) and lacking cilia.

Symphyodon leiocarpus, however, differs from the other species of Symphyodon in the followings (character states observed only in the latter are shown in square brackets): 1) laminal cells of stem and branch leaves smooth [more or less prorate or prorulose, often spinose, at upper ends], 2) axillary hairs uniseriate, (4 or) 5-celled; upper (2 or) 3 cells elongate, hyaline and basal 2 cells quadrate, brownish [brownish or hyaline, uniseriate, 2 or (rarely) 3-celled, with a single, quadrate, basal cell], 3) capsule walls smooth [echinate or spinose], 4) stomata superficial [immersed], and 5) spores 20–25 μ m in diameter [12–20 μ m in diameter]. These features, we consider, clearly suggest Symphyodon leiocarpus to be remotely related to other members of the genus Symphyodon. In addition, we noticed that Symphyodon leiocarpus shows a different habitat preference. The other species of Symphyodon grow on the branches of undergrowth shrubs in well preserved forests, while Symphyodon leiocarpus is restricted to sunnier places, such as the base of tree trunks and on the branches of shrubs at the edge of thickets and on the higher branches of tall trees. These differences are not sufficient, however, to classify Symphyodon leiocarpus in a separate genus because species with widely different features often form monophyletic groups and autoapomorphies cannot be used to infer phylogenetic affinity. For example, species with echinate and smooth capsules sometimes belong to the same genus (e.g. in Chaetomitrium, Akiyama & Suleiman 2001).

Comparison with other genera in the Symphyodontaceae

Based on morphological features and molecular analyses, Goffinet *et al.* (2008) listed five genera in the Symphyodontaceae. Along with *Symphyodon*, they are *Chaetomitriopsis* M. Fleisch., *Chaetomitrium* Dozy & Molk., *Dimorphocladon* Dixon, *Trachythecium* M. Fleisch., and *Unclejackia* Ignatov, T.J. Kop. & D.H. Norris. Among

them, Chaetomitriopsis, Chaetomitrium and Unclejackia resemble each other in their gametophytic features, while Symphyodon leiocarpus shares only the following features with them; (1) reduced endostome, (2) weakly differentiated alar regions, and (3) elongated vaginula after fertilization (Ignatov et al. 1999). As for Trachythecium, its pendent capsules with a perfect Hypnum-type peristome and mammillose exothecial cells might indicate a remote relationship to Symphyodon leiocarpus. According to our field observations on the Borneo Island, the monospecific genus Dimorphocladon is unique in living on the leaves of shrubs growing beside streams and rivers. Its upright, more or less flat branches with attenuate tips bearing filamentous gemmae in the leaf axils give Dimorphocladon an appearance similar to species of Clastobryopsis M. Fleisch. [Akiyama 1993 (as Aptychella sp.), Akiyama 1997]. Although Dixon (1922) pointed out the affinity between Dimorphocladon and Chaetomitrium, we do not consider the long, smooth setae, cylindrical capsules, long-beaked opercula, and filamentous gemmae of Dimorphocladon to suggest a close relationship. As a result, Symphyodon leiocarpus shares most morphological features with other species of Symphyodon.

Comparison with other families

Upright capsules with more or less reduced endostomes, leaves with obtuse or widely acute apex and often bifid costa as well as the epiphytic habitat of *Symphyodon leiocarpus* suggest affinity to member of the Entodontaceae, especially to *Entodon* Müll. Hal. *Symphyodon leiocarpus*, however, does not have features found in *Entodon*, such as the wide alar regions with numerous, small, quadrate cells, cylindrical capsules, and much reduced, fragmented endostome often adhering to the inner surface of exostome teeth.

Symphyodon leiocarpus also appears similar to some members of the Hylocomicaceae, especially to those with bi- or tripinnately branched stems and/or upright capsules, which can be summarized as follows:

Leptohymenium Schwägr. Although the Asian representative of Leptohymenium, L. tenue

90

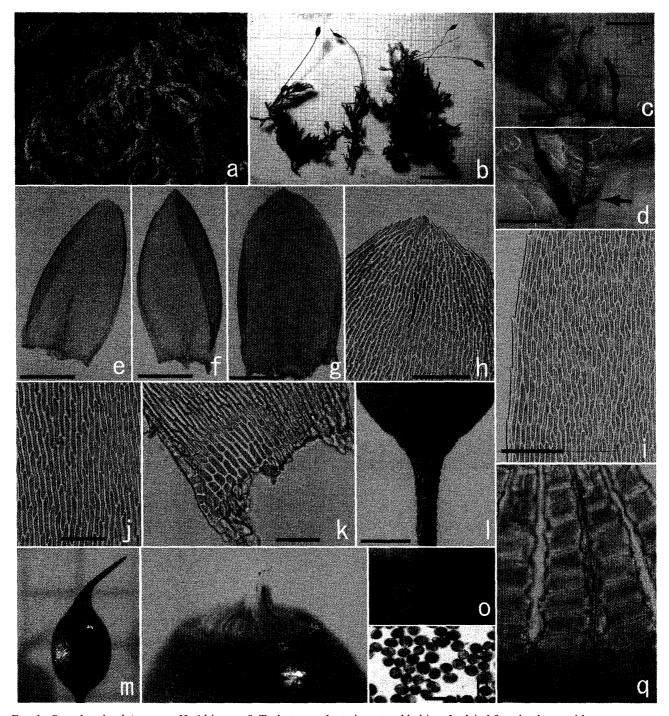


Fig. 1. Symphyodon leiocarpus H. Akiyama & Tsubota. a: plants in natural habitat. b: dried female plants with mature sporophytes. c: female plant with elongated vaginula in wet condition. d: elongated vaginula after fertilization (arrow indicates unfertilized perichaetium). e & f: branch leaves. g: stem leaf. h: apex of branch leaf. i: upper margin of branch leaf. j: median laminal cells of branch leaf. k: alar region of branch leaf. l: capsule neck and mammillose, uppermost portion of a seta. m: a mature capsule with oblique beaked operculum. n: closeup of dried peristome. o: superficial stomata at neck of capsule. p: spores. q: outer surface of lanceolate exostome teeth and filamentous endostome segments. Scales = 5 mm in a, b & c, 1 mm in d, 0.35 mm in e-g, 0.5 mm in m & n, and 50 μm in h-k, o-q.

September 2009

(Hook.) Schwägr., has upright capsules, they are not ovoid but long cylindrical. Additionally, the presence of prostome (pro-peristome) as irregular deposits on the outer surface of the exostome teeth and well-differentiated decurrent alar regions also suggest a remote relationship.

Leptocladiella M. Fleisch. Rather delicate and simple shoots with few lateral branches give a unique appearance to Leptocladiella among the Hylocomiaceae. While Symphyodon leiocarpus is more or less bi- or tri-pinnately branched. According to Rohrer (1995), the costa of the branch leaves is often single and ends in a spine and the outer surfaces of exostome teeth are basally striate in Leptocladiella psilura (Mitt.) M. Fleisch.

Macrothamnium M. Fleisch. A number of species have been reported under Macrothamnium. Most of them are characterized by having more or less sub-arcuate capsules, and finely striate exostome teeth. The sole exception is M. leptohymenioides Nog., which has upright and subglobose capsules (Noguchi 1972b). The long, double costa, distinctly dentate leaf margins, shortly beaked operculum and the basally finely striate exostome teeth, however, are quite different from those found in Symphyodon and in S. leiocarpus.

Orontobryum Mitt. ex M. Fleisch. resembles Symphyodon leiocarpus in the upright, globose capsules. The paraphyllia on the stems and branches, monopodial branching pattern, strong dentition of the leaf margins, and dome shaped opercula with scarcely elongate beaks (Rohrer 1985), however, may indicate a remote relationship to both Symphyodon in general and to S. leiocarpus in particular.

Molecular Phylogenetic Analysis and Its Implications

To clarify the phylogenetic position of *Symphyodon leiocarpus*, we carried out molecular phylogenetic analyses based on chloroplast *rbc*L gene sequences (Fig. 2 and Appendix). We selected three species of *Symphyodon*, one each from the three infrageneric groups recognized by He & Snider (1992). They were collected from the

same locality on Doi Inthanon, along with an additional sample of *S. scaber* from Myanmar.

Leptohymenium (Symphyodon oblongifolius was once classified there) and related genera of the Hylocomiaceae as well as species of Entodon were also included in the analysis because they show morphological similarities to Symphyodon. Other OTUs are detailed in the Appendix.

Investigation of topology candidates were performed with the following programs: MEGA 4 (Tamura et al. 2007, Kumar et al. 2008), Molphy 2.3b3 (Adachi & Hasegawa 1996), MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003), PAUP* 4.0b10 (Swofford 2003), PAUPRat (Sikes & Lewis 2001) over PAUP, PhyML 2.4.4 (Guindon & Gascuel 2003). Kakusan3 (Tanabe 2007) was used to select the nucleotide substitution model for the data set. Recalculation of likelihood values for each tree topology was performed with PAUP. The candidate topologies were evaluated by the approximate unbiased test (AU; Shimodaira 2002, 2004) using CONSEL (Shimodaira & Hasegawa 2001). Procedures of sequencings, alignments, and phylogenetic analysis adopted are nearly the same as detailed in Tsubota et al. (2004, 2005) and Ozeki et al. (2007).

The phylogeny of Symphyodon and its allies is shown in Fig. 2 based on the alignment of 1,220 bps of the 42 moss chloroplast rbcL gene sequences, depicted by the best-supported tree with high ranking log-likelihood values that passed the approximate unbiased test (AU; Shimodaira 2000, 2002). Four samples (three species) of Symphyodon formed a monophyletic clade with S. leiocarpus appearing as sister to the clade with high supporting values (AU/LBP/BPmp/BPnj/ BPml/PP = 100/100/99/100/100/1.00; abbreviations of these values are explained in the legend for Fig. 2). The results support our supposition based on morphological comparisons that S. leiocarpus is heterogeneous among members of Symphyodon.

Since we were not able to include any samples from the Symphyodontaceae except for *Symphyodon*, it is still ambiguous whether *Symphyodon leiocarpus* should be treated in a genus separate

AU/LBP/BPmp/BPnj/BPmI/PP

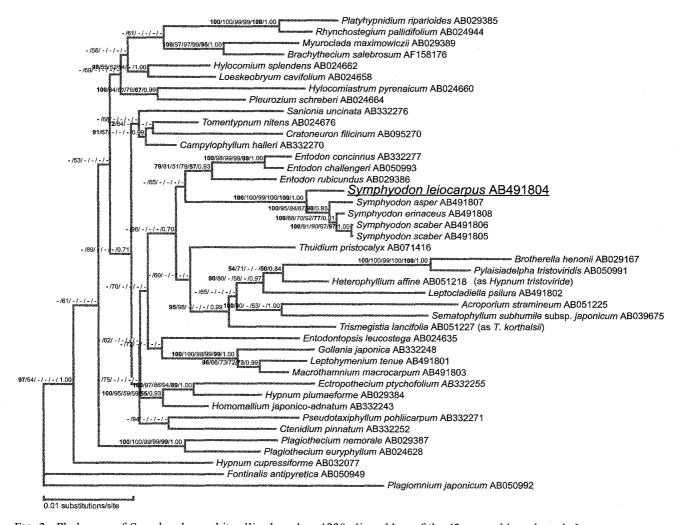


FIG. 2. Phylogeny of Symphyodon and its allies based on 1220 aligned bps of the 42 moss chloroplast rbcL gene sequences, depicted by the best-supported tree (GTR + G model; ln L = -5910.4) with highest log-likelihood value that passed the approximate unbiased test (AU; Shimodaira 2002, 2004) by CONSEL. The root is arbitrarily placed on the branch leading to Plagiomnium japonicum. The horizontal length of each branch is proportional to the estimated number of nucleotide substitutions. Supporting values greater than 50% (AU/LBP/BPmp/BPnj/BPml/PP) are shown near the nodes: the AU probabilities based on AU test using the multiscale bootstrap technique (AUs in %); local bootstrap probabilities calculated with the estimation using the RELL resampling method (Kishino et al. 1990, Hasegawa & Kishino 1994) by Molphy 2.3b3 with TN93 model (LBPs; in %); classical bootstrap probabilities (Felsenstein 1985) based on 10,000 replications calculated with MP and NJ methods by MEGA 4 with maximum composite likelihood model (BPmps and BPnjs; in %); and bootstrap probabilities based on 1,000 replications calculated with ML method by PhyML with GTR + G model (BPmls; in %); and the Bayesian posterior probability calculated by the Bayesian information criterion (BIC) approximation (Schwarz 1978, Hasegawa & Kishino 1989) by MrBayes with GTR + G model (PPs).

from *Symphyodon* or not. Relatively short branches among the five samples, if compared to other congeneric cases in *Entodon* and *Plagiothecium* in the present analysis, however, might support the latter placement.

Affinities to the Entodontaceae and Hylocomiaceae based on molecular analysis

The tree shows a relationship between *Symphyodon* (including *S. leiocarpus*) and *Entodon*, although the supporting values are low. Because of insufficient taxon sampling their relationships

September 2009

are unclear; some topologies with high likelihood values showed a close relationship between *Entodon* and other genera and families, such as *Thuidium* and the Sematophyllaceae, as shown by Tsubota *et al.* (2004).

None of the members of the Hylocomiaceae (Hylocomium, Hylocomiastrum, Leptohymenium, Leptocladiella, Loeskeobryum, Macrothamnium, and Pleurozium) is closely related to the (Symphyodon + S. leiocarpus) clade in the present analysis as was already shown by Goffinet et al. (2008). In addition, these seven genera are remotely separated into three different clades, which may suggest paraphyly.

Taking into consideration the evidence discussed above, we conclude that the *Symphyodon leiocarpus* should be treated as new and that it represents a new subgenus within *Symphyodon*.

Taxonomic Treatment

Symphyodon subg. Macrothamniopsis H. Aki-yama & Tsubota, subg. nov.

Affinis *Symphyodonti* subg. *Symphyodonti*, sed capsulis laevibus stomatibus superficialibus sporis majoribus, $20-25 \mu m$ diametro diversus.

Typus. Symphyodon leiocarpus H. Akiyama & Tsubota

Symphyodon leiocarpus H. Akiyama & Tsubota, **sp. nov.** (Fig. 1a-q)

Affinis Symphyodonti erinaceo, sed capsulis laevibus diversus.

Typus. THAILAND, Chiang Mai, Doi Inthanon, around the summit, monument trail, 2550 m alt., Dec. 5, 2000, *H. Akiyama Th-51* (holo- BKF; iso- BM, CMU, HIRO, HYO, L, MO, NY, SING).

Plants green or olive-green, older parts turning yellow, 2–3 cm long, monopodially branched, prostrate, with a number of short ascending shoots, forming dense mats on substrata, subdendroid, more or less regularly bi- or tripinnately branched; branches terete or sometimes slightly complanately foliate, usually 0.5–1.0 cm long; central strands absent or weakly developed; cortical cells lax, thin walled, epidermal cells thick walled, with substereids, tinged reddish brown in

age; paraphyllia and pseudoparaphyllia absent. Rhizoids restricted to ventral surface of prostrate shoots, tufted, smooth, brown. Stem leaves ovatelanceolate, ca. 1 mm long, obtuse or broadly acute, upper surface often concave, neither plicate nor rugose; margins minutely crenulate; costa double or more or less branched, reaching 1/3-1/2 leaf length, rarely obscure; uppermost laminal cells shortly rhomboid, evenly thick walled, smooth; median laminal cells linear-rhomboid, evenly thick walled, $40-60 \mu m$ long, smooth; marginal laminal cells becoming narrower, smooth; alar region differentiated with small subquadrate cells. Axillary hairs hyaline, uniseriate, (4 or) 5-celled; upper (2 or) 3 cells elongate, hyaline, smooth; basal 2 cells quadrate, brownish. Branch leaves similar to stem leaves in shape and size; terminal branch leaves much smaller than stem and branch leaves, shortly ovate, ca. 0.5-0.7 mm long, upper surface deeply concave, broadly obtuse, often minutely apiculate; uppermost laminal cells shortly rhomboid, median laminal cells $30-60 \mu m$ long, smooth; margins minutely crenulate; alar cells weakly differentiated. Dioicous: male plants slightly more slender than female plants. Perigonia on ascending shoots (usually on secondary and terminal branches), containing 3–5 antheridia. *Perigonial leaves* shortly ovate, concave, to 0.6 mm long, ecostate. Perichaetia sessile, restricted to ascending stems and secondary branches. Perichaetial leaves gradually narrowed from ovate to oblong sheathing base, ecostate. Vaginula much elongated after fertilization and becoming a short distinct branch. Calyptrae unknown. Setae reddish brown, 5-6 mm long, almost always straight (rarely slightly curved downward at distal end), mammillate just below neck. Capsules globose or shortly ovoid, upright, surface smooth, reddish brown, slightly glossy; exothecial cells hexagonal, evenly thick walled; annulus differentiated in 2 or 3 rows; stomata 6–15 per capsule, superficial, restricted to neck. Opercula obliquely narrowly rostrate. Peristome double, opening outwards in moist conditions. Exostome teeth 16, brownish yellow, apically pale white, narrowly lanceolate, median furrow absent, $400-500 \mu m$ long, finely papillose throughout on both surfaces. *Endostome* with low basal membrane, segments linear, lacking perforations, $200-300 \mu m$ long, finely papillose; cilia absent. *Spores* spherical, greenish, finely papillose, $20-25 \mu m$ in diameter.

Distribution. Myanmar (Chin State), Thailand (Chiang-Mai Co.).

Habitat. Forming small patches on base of tree trunks and on branches of shrubs and small trees (sometimes pendulous) in mossy or evergreen upper montane forests. Often intermingled with Macrothamnium submacrocarpum and other species of Symphyodon.

Distinguishing features. 1) leaves ovate-lanceolate, concave, obtuse or broadly acuminate with double or more or less branched costa, 2) alar regions weakly developed with quadrate cells, 3) laminal cells linear, evenly thick walled, and totally smooth, 4) axillary hairs uniseriate with a single basal cell, 5) capsules upright, totally smooth, 6) stomata superficial, and 7) spores 20–25 µm in diameter.

Paratypes. THAILAND. Chiang Mai: Doi Inthanon, around the summit, monument trail, 2550 m alt, H. Akiyama Th-127 & Th-128 (HYO!), A. Touw 9780 (L!); ibid., Ang Ka trail, 2550 m alt., H. Akiyama Th-34 & Th-42 (HYO!), H. Akiyama 21551 & 21552 (HYO!); ibid., Kew Mae Pan nature trail, 2200 m alt., H. Akiyama 21576 (HYO!); ibid., 2300 m alt., A. Touw 10128 (L!); ibid., 2150–2250 m alt., A. Touw 10250 (L); ibid., 2150–2200 m alt., A. Touw 10010 (L!); ibid., 1600–1650 m alt., H. Akiyama, M. Kanzaki, T. Irie & H. Ando 314 & 332 (BKF!, CMU!, HYO!); Doi Suthep, summit of Doi Pui, 1600–1650 m alt., A. Touw 8539 (L!).

MYANMAR. Chin State: Natma-Taung National Park, Mt. Victoria, 2470 m alt., *J. Murata et al. 23262* (HYO!).

Note. Touw (1968) also reported Symphyodon leiocarpus from Doi Chiang Dao, Chiang Mai Co., Thailand (A. Touw 9380, L), but we have not examined the specimen.

We thank Mr. M. Thawatchai (Royal Forest Department) and Dr. Kanya Santanachote (Chiang Mai University) who helped us in the field surveys. We also thank Drs. U. Mizushima for comparing our specimens with *Entodon*, B. C. Tan and A. Touw for their suggestions on the identity of the plants, and Drs. A. Newton (BM), W. R. Buck (NY), X. He-Nygrén (H), A. Touw (L), C. Rausch (PC),

and H. Deguchi (HIRO) for searching for the holotype of *Leptohymenium oblongifolius*. We also thank the Analysis Center of Life Science, Hiroshima University, for help in sequencing and the Natural Science Center for Basic Research and Development, Hiroshima University, for supplying cryogen, Dr. W. R Buck, The New York Botanical Garden, and Dr. D. Boufford, Harvard University Herbaria, for correcting the English text, and two anonymous referees for their valuable suggestions on the draft. This study was financially supported by Grants-in-Aid from the Japanese Ministry of Education, Culture, Sports, Science and Technology (No.18570092) to the senior author, (No.09041165 and 13375003) to Dr. J. Murata (Tokyo University) and (No. 20405008) to Dr. M. Kanzaki (Kyoto University).

References

Adachi, J. & M. Hasegawa. 1996. MOLPHY version 2.3: programs for molecular phylogenetics based on maximum likelihood. Computer Science Monographs 28: 1–150.

Akiyama, H. 1993. Taxonomic studies of mosses of Seram and Ambon (Moluccas, East Malesia) collected by Indonesian-Japanese botanical expeditions. VII. Lembophyllaceae, Splachnaceae, Myuriaceae, Neckeraceae, Brachytheciaceae Amblystegiaceae and Sematophyllaceae, with additions to previous reports on Dicranaceae and Pterobryaceae. J. Fac. Sci. Univ. Tokyo, Bot. 15: 219–254.

Akiyama, H. 1997. Taxonomic studies of mosses of Seram and Ambon (Moluccas, East Malesia) collected by Indonesian-Japanese Botanical Expeditions VIII. Meteoriaceae, Hookeriaceae, and Trachypodaceae. Human and Nature 2: 9–31.

Akiyama, H. 2006. New records of mosses from Thailand. Trop. Bryol. 28: 59.

Akiyama, H. & M. Suleiman. 2001. Taxonomical notes on the genus *Chaetomitrium* (Hookeriaceae, Musci) of Borneo. Hikobia 13: 491–509.

Akiyama, H. & H. Tsubota. 2001. *Pseudotrismegistia* H. Akiy. & Tsubota, a new genus for the Sematophyllaceae. Acta Phytotax. Geobot. 52: 85–95.

Akiyama, H. & H. Tsubota. 2004. Morphological and genetical variations and familial affinity of the genus *Dixonia* (Musci). Bryol. Res. 8: 229–237.

Dixon, H. N. 1922. Some new genera of mosses. J. Bot. 60: 101–110.

Dixon, H. N. 1932. On the moss flora of Siam. J. Siam Soc., Nat. Hist. Suppl. 9: 1–51.

Dixon, H. N. 1935. Further contributions to the moss flora of Siam. J. Siam Soc., Nat. Hist. Suppl. 10: 1–30.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791. Gangulee, H.C. 1977. Mosses of eastern India and adja-

- cent regions. Fascicle 6. Privately published, Calcutta.
- Goffinet, B., W. R. Buck & A. J. Shaw. 2008. Morphology and classification of the Bryophyta. *In*: Goffinet, B. & A. J. Shaw (eds.), Bryophyte Biology (2nd edition), pp. 55–138. Cambridge Univ. Press, Cambridge.
- Guindon, S. & O. Gascuel. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Syst. Biol. 52: 696–704.
- Hara, M. 2003. Vegetation of Doi Inthanon, northern Thailand. Trop. Ecol. Letters no. 51: 1–6. (in Japanese)
- He, Si. [Internet resource]. Checklist of the mosses of Thailand. http://www.mobot.org/MOBOT/moss/Thailand (September 13, 2008).
- He, Si & J. Snider. 1992. A preliminary survey of the moss genus *Symphyodon* (Symphyodontaceae, Musci). Bryobrothera 1: 283–287.
- He, Si & J. Snider. 2000. A taxonomic revision of *Symphyodon* (Musci: Symphyodontaceae). Bryologist 103: 52–81.
- Horikawa, Y. & H. Ando. 1964. Contributions to the moss flora of Thailand. Nat. Life Southeast Asia 3: 1–44.
- Huelsenbeck, J. P. & F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17: 754–755.
- Ignatov, M. S., T. Koponen & D. H. Norris. 1999. Bryophyte flora of the Huon Peninsula. LXII. Brachytheciaceae (Musci), excluding *Homalothecium* and *Palamocladium*. Acta Bot. Fennica 165: 23–72.
- Kishino, H., T. Miyata & M. Hasegawa. 1990. Maximum likelihood inference of protein phylogeny and the origin of chloroplasts. J. Mol. Evol. 30: 151–160.
- Kitagawa, N. 1967a. Studies on the Hepaticae of Thailand I. The genus *Bazzania*, with general introduction. J. Hattori Bot. Lab. 30: 249–270.
- Kitagawa, N. 1967b. Researches of hepatics in Thailand. Nat. Life SE Asia. 4: 180–183. (in Japanese)
- Noguchi, A. 1972a. Mosses of Thailand. Lindbergia 1: 169–183.
- Noguchi, A. 1972b. A revision of the genus *Macrothamnium*. Kumamoto J. Sci. Biol. 11: 1–12.
- Noguchi, A. 1973. Contributions to the bryology of Thailand. J. Hattori Bot. Lab. 37: 235–250.
- Ogawa, H., K. Yoda & T. Kira. (1961). A preliminary survey on the vegetation of Thailand. Nat. Life SE Asia 1: 21–157.
- Ozeki, M., Y. Isagi, H. Tsubota, P. Jacklyn & D. M. J. S. Bowman. 2007. Phylogeography of an Australian ter-

- mite, *Amitermes laurensis* (Isoptera, Termitidae), with special reference to the variety of mound shapes. Mol. Phyl. Evol. 42: 236–247.
- Renauld, F. & J. Cardot. 1896[1895]. Musci exotici novi vel mixus cogniti VII. Bull. Soc. Bot. Belgique 34: 57–78.
- Rohrer, J. H. 1985. A generic revision of the Hylocomiaceae. J. Hattori Bot. Lab. 59: 241–278.
- Ronquist, F. & J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.
- Schwartz, G. 1978. Estimating the dimension of a model. Ann. Stat. 6: 461–464.
- Shimodaira, H. 2002. An approximately unbiased test of phylogenetic tree selection. Syst. Biol. 51: 492–508.
- Shimodaira, H. 2004. Approximately unbiased tests of regions using multistep-multiscale bootstrap resampling. Ann. Stat. 32: 2616–2641.
- Shimodaira, H. & M. Hasegawa. 2001. CONSEL: for assessing the confidence of phylogenetic tree selection. Bioinformatics 17: 1246–1247.
- Sikes, D. S. & P. O. Lewis. 2001. PAUPRat: PAUP* implementation of the parsimony ratchet, beta software, version 1. Distributed by the authors. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, USA.
- Swofford, D. L. 2003. PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4. Sinauer Associates, Sunderland.
- Tamura, K., J. Dudley, M. Nei & S. Kumar. 2007. MEGA4: molecular evolutionary genetics analysis (MEGA) software version 4.0. Mol. Biol. Evol. 24: 1596–1599.
- Tanabe, A. S. 2007. KAKUSAN: a computer program to automate the selection of a nucleotide substitution model and the configuration of a mixed model on multilocus data. Mol. Ecol. Notes 7: 962–964.
- Tsubota, H., E. De Luna, D. Gonzalez, S. M. Ignatov & H. Deguchi. 2004. Molecular phylogenetic and ordinal relationships based on analyses of a large-scale data set of 600 *rbcL* sequences of mosses. Hikobia 14: 149–169.
- Tsubota, H., K. Takahashi, M. Nakahara, H. Mohamed & H. Deguchi. 2005. A simple procedure for DNA isolation using small quantities of lichen thallus. Lichenology 4: 25–28.
- Touw, A. 1968. Miscellaneous notes on Thai mosses. Nat. Hist. Bull. Siam Soc. 22: 217–244.

Received April 21, 2009; accepted June 10, 2009

APPENDIX. Taxon sampling and DDBJ/EMBL/GenBank accession numbers used in the present analysis (Fig. 2). Newly obtained sequences (in **bold**) are shown with their voucher information (in order of scientific name, accession number, locality, and collector number). All voucher specimens of newly sequenced samples are deposited in HYO.

Acroporium stramineum (Reinw. & Hornsch.) M. Fleisch., AB051225; Brachythecium salebrosum (Hoffm. ex F. Weber & D. Mohr) Schimp., AF158176; Brotherella henonii (Duby) M. Fleisch., AB029167; Campylophyllum halleri (Sw. ex Hedw.) M. Fleisch., AB332270; Cratoneuron filicinum (Hedw.) Spruce, AB095270; Ctenidium pinnatum (Broth. & Paris) Broth., AB332252; Ectropothecium ptychofolium N. Nishim., AB332255; Entodon challengeri (Paris) Cardot, AB050993; E. concinnus (De Not.) Paris, AB332277; E. rubicundus (Mitt.) A. Jaeger, AB029386; Entodontopsis leucostega (Brid.) W.R. Buck & Ireland, AB024635; Fontinalis antipyretica Hedw., AB050949; Gollania japonica (Cardot) Ando & Higuchi, AB332248; Heterophyllium affine (Hook.) M. Fleisch., AB051218; Homomallium japonicoadnatum (Broth.) Broth., AB332243; Hylocomiastrum pyrenaicum (Spruce) M. Fleisch., AB024660; Hylocomium splendens (Hedw.) Schimp., AB024662; Hypnum cupressiforme Hedw., AB032077; Hypnum plumaeforme Wilson, AB029384; Loeskeobryum cavifolium (Sande Lac.) M. Fleisch. ex Broth., AB024658; Leptohymenium tenue (Hook.) Schwägr., AB491801, Myanmar, Mt. Victoria, 2750 m alt., J. Murata et al. 22298; Leptocladiella psilura (Mitt.) M. Fleisch., AB491802, Myanmar, Mt. Victoria, 3000 m alt., J. Murata et al. 22380; Macrothamnium macrocarpum (Reinw. & Hornsch.) M. Fleisch., AB491803, Thailand, Doi Inthanon, around the summit, 2550 m alt., H. Akiyama Th-65; Myuroclada maximowiczii (G.G. Borshch.) Steere & W.B. Schofield, AB029389; Plagiothecium nemorale (Mitt.) A. Jaeger, AB029387; P. euryphyllum (Cardot & Thér.) Z. Iwats., AB024628; Plagiomnium japonicum (Lindb.) T.J. Kop., AB050992; Platyhypnidium riparioides (Hedw.) Dixon, AB029385; Pleurozium schreberi (Willd. ex Brid.) Mitt., AB024664; Pseudotaxiphyllum pohliaecarpum (Sull. & Lesq.) Z. Iwats., AB332271; Pylaisiadelpha tristoviridis (Broth.) Afonina, Tsubota & Ignatova, AB050991 [submitted as Hypnum tristoviride (Broth.) Paris]; Rhynchostegium pallidifolium (Mitt.) A. Jaeger, AB024944; Sanionia uncinata (Hedw.) Loeske, AB332276; Sematophyllum subhumile (Müll. Hal.) M. Fleisch. subsp. japonicum (Broth.) Seki, AB039675; Symphyodon asper (Mitt.) A. Jaeger, AB491807, Thailand, Doi Inthanon, around the summit, 2550 m alt., H. Akiyama 21543; Symphyodon erinaceus (Mitt.) A. Jaeger, AB491808, Thailand, Doi Inthanon, Kew Mae Pan, 2200m alt., H. Akiyama 21562; Symphyodon leiocarpus H. Akiyama & Tsubota, AB491804 [submitted as Symphyodon sp.], Thailand, Doi Inthanon, around the summit, H. Akiyama Th-127; Symphyodon scaber (Tixier) S. He & Snider, AB491805, Myanmar, Mt. Victoria, 2250 m alt., J. Murata et al. 23237; Symphyodon scaber, AB491806, Thailand, Doi Inthanon, Kew Mae Pan, 2200 m alt., H. Akiyama 21559; Thuidium pristocalyx (Müll. Hal.) A. Jaeger, AB071416; Tomentypnum nitens (Hedw.) Loeske, AB024676; Trismegistia lancifolia (Harv.) Broth., AB051227 [submitted as T. korthalsii (Dozy & Molk.) Broth.].